# BRIEF ARTICLES

*Mycologia*, 81(4), 1989, pp. 622–626.


## *PALAEOFIBULUS GEN. NOV.*, A CLAMP-BEARING FUNGUS FROM THE TRIASSIC OF ANTARCTICA

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Reports of fossil fungi have been relatively infrequent until recently. During the last decade, however, there has been an increasing number of studies which have focused on fossil fungi and now provide a reasonable data base (*e.g.*, Stubblefield and Taylor, **1988**, and references therein). Included are both vegetative and reproductive structures which encompass several major taxonomic groupings.

Of these fungal remains the presence of clamp connections is restricted to only a few reports. *Palaeancistrus martinii* Dennis (**1970**), known from Middle Pennsylvanian sediments, was the first clamp-bearing fungus described. This fungus is regarded as a saprophytic basidiomycete based on its occurrence within the xylem of the coenopterid fern *Zygopteris*. Another clamp-bearing fungus from the Middle Pennsylvanian is *Palaeosclerotium* Rothwell (**1972**). The presence of ascomycete-like reproductive structures (asci) in addition to subsequently identified clamp connections was the basis upon which Dennis (**1976**) suggested that this fungus represented an evolutionary intermediate between modern ascomycetes and basidiomycetes. However, McLaughlin (**1976**) suggested a more cautious assessment of *Palaeosclerotium*. McLaughlin questioned Dennis' (**1976**) interpretations of the dolipore septum and clamp connections of this fossil in addition to contending that *Palaeosclerotium* may represent two separate fungi, a view also originally considered by Dennis. Later, Singer (**1977**) reexamined the type material and concurred with Dennis' (**1976**) assertions as well as suggesting that *Palaeosclerotium* shared affinities with a modern ascomycete order, the Eurotiales. Other fungi associated with gymnospermous wood from the Triassic of Antarctica have been reported with both simple and medallion clamp connections (Stubblefield and Taylor, **1986**). Wood decay in the Devonian progymnosperm *Callixylon* was also suggested as the result of an ascomycetous or basidiomycetous fungus (Stubblefield *et al.*, **1985**). Although true clamps were not substantiated on these hyphae, presence of occasional intercalary bulges along hyphal margins were suggestive of clamps.

The intent of this paper is to report occurrence of a clamp-bearing fungus, consisting of septate hyphae and chains of spores, from the Triassic of Antarctica.

### MATERIALS AND METHODS

Several specimens of fungi have recently been discovered associated with plant remains within a silicified peat collected from the Fremouw Formation in Antarctica. The stratigraphic position of these sediments is considered Early- to Middle-Triassic based on occurrence of the vertebrate genera *Lystrosaurus* and *Cynognathus* and recent palynological studies (Farabee *et al.*, **1989**). Light microscope slides were prepared from cellulose acetate peels of rock surfaces, which had

been etched with hydrofluoric acid, following the techniques of Smoot *et al.* (**1985**). Fossil materials (slides, peels, and slabs) are housed in The Ohio State University Paleobotanical Collection under acquisition nos. 14,456–14,476.

**Palaeofibulus** Osborn, Taylor *et* White, *gen. nov.*
(Diagnosis same as for type species.)

**Palaeofibulus antarctica** Osborn, Taylor *et* White, *sp. nov.* FIGS. 1–8

*Species diagnosis.*—Fossil mycelium composed of branched, septate hyphae ranging from 6.2–7.5 μm diam; hyphal filaments with clamp connections between some elements; clamps between 1.25–2.5 μm diam, some septate; spores thick-walled, ellipsoidal to globose, 17.5–23.8 × 30–32.5 μm, produced in chains or clumps and attached individually by small disjunctor cells; wall psilate.

HOLOTYPE: Ohio State University Paleobotanical Collection No. 10,216, D top α (FIGS. 1–8).

COLLECTION LOCALITY: Fremouw Peak, Antarctica, near the Beardmore Glacier.

STRATIGRAPHIC POSITION: Fremouw Formation, Beacon Supergroup.

AGE: Early–Middle Triassic.

ETYMOLOGY: Genus—Greek, *palaios* (ancient) and Latin, *fibula* (clamp); specific epithet—after collection locality.

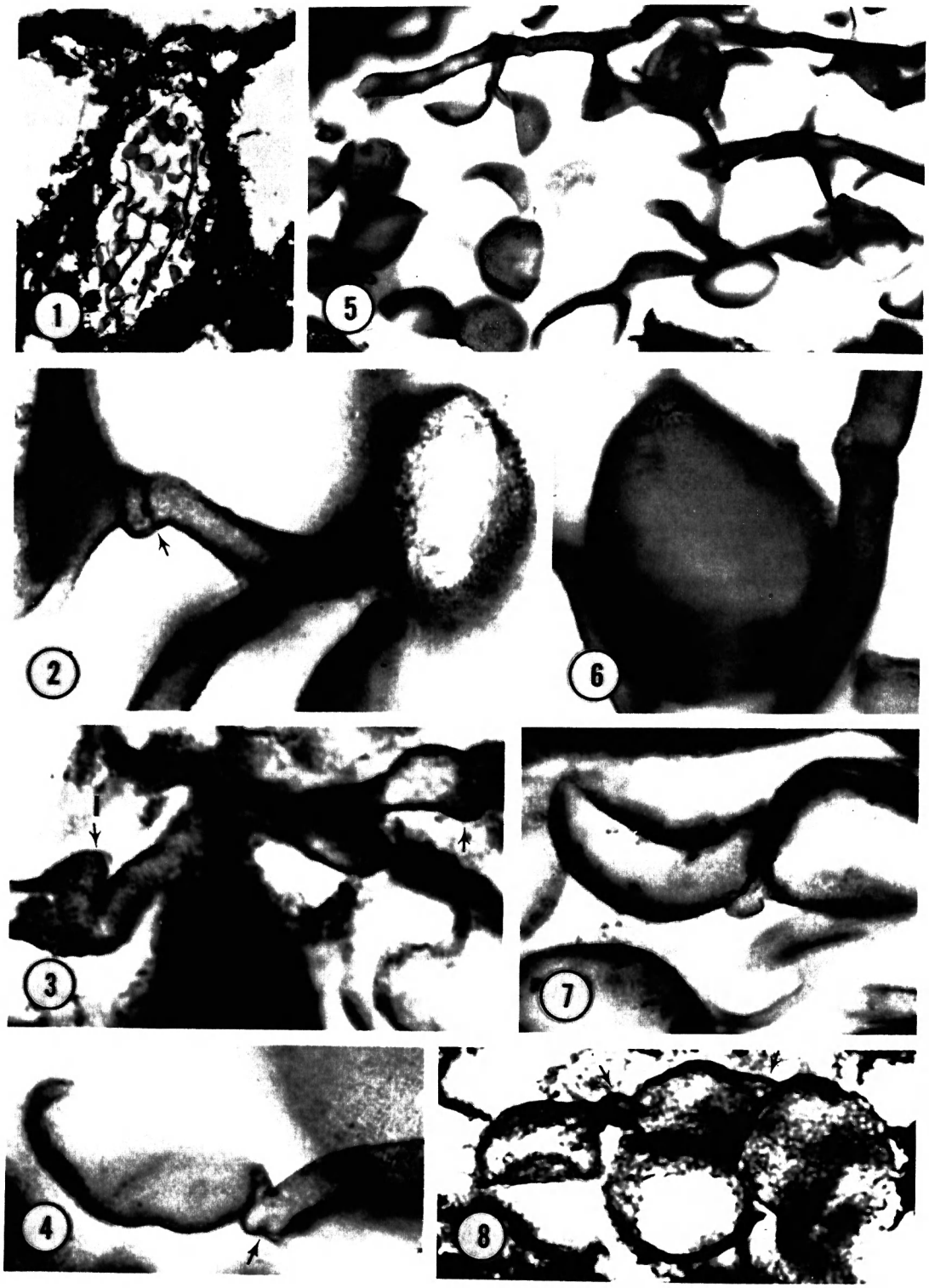
## DESCRIPTION

Specimens of *Palaeofibulus* were discovered within the lacunar canal of an unidentified stem axis (FIG. 1) and the mesophyll of an adjacent, disarticulated leaf. The fungus consists of branching, septate hyphae and chains of spores (FIG. 5). Hyphal filaments range from 6.2–7.5 μm diam and possess clamp connections at some septa (FIG. 2). Clamps range from 1.25–2.5 μm diam and are also septate (FIGS. 2, 6). In addition to well-defined clamps, an incomplete clamp is present along one hyphal strand (FIG. 3). Spores, when seen in lateral surface view, are ellipsoidal to globose and vary from 17.5–23.8 × 30–32.5 μm (FIGS. 6, 7). They appear to be produced either in chains or clumps and are attached to each other by small, intercalary disjunctors of hyphae (FIGS. 4, 7, 8). Attachment and thick spore wall can more easily be observed in sectional view (FIG. 4).

## DISCUSSION

Presence of clamp connections along the hyphae of *Palaeofibulus* suggests that the preserved mycelial state was dikaryotic. Inference of a dikaryotic nature purely on the basis of clamps is generally accepted (Webster, **1970**). However, the incomplete clamp demonstrated by *Palaeofibulus* (FIG. 3) does not meet the functional criteria of a true clamp connection. Regarding this structure, two interpretations can be postulated. One interpretation views the incomplete clamp as representing an intermediate stage in the developmental sequence of clamp formation. A second explanation is that it represents a pseudoclamp, a cytogenetically induced structure found in some extant basidiomycetes (Rosinski and Robinson, **1968**). Dennis (**1970**) identified incomplete clamps in *Palaeancistrus* as pseudoclamps. This identification was based primarily on the occurrence of multiple, successive pseudoclamps along one hyphal filament and the author's reservations concerning the fossilization potential of such a short-lived developmental phase. We believe, however, that the incomplete clamp observed in *Palaeofibulus* does indeed represent an ontogenetic stage of clamp formation because the hyphal filament which contains the incomplete clamp also possesses complete clamps (FIG. 3).

If the assumption of dikaryotic mycelium is accepted, then spores of *Palaeofibulus* can be interpreted as either dikaryotic propagules or as temporary binucleate structures in which karyogamy and subsequent meiotic divisions occur. Several groups of extant fungi have reproductive stages which could be postulated as modern analogs to those observed in *Palaeofibulus*. For example, contemporary rusts produce a variety of dikaryotic spore stages, some of which are separated by dikaryotic, intercalary cells or disjunctor cells (Rijkenberg and Truter, **1974**). Several extant hyphomycetes also possess clamp connections and dikaryotic conidia. Some of these fungi have been suggested to be conidial basidiomycetes and include *Pagidospora* (Drechsler, **1960**), *Aegerita candida* (Webster and Descals, **1981**), *Naiadella* (Marvanová and Bandoni, **1987**), and *Fibulotaeniella* and *Taeniospora nasifera* (Marvanová and Bärlocher, **1988**). Furthermore, numerous fungi produce spores in chains or clumps interspersed by disjunctor cells as well as thick-walled resting conidia or chla-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mydospores. One of the perplexing aspects of investigating fossil fungi is the difficulty in interpreting the nature of spores. In the case of *Palaeofibulus,* this is particularly difficult because in the absence of unequivocal sexual stages, the preserved spores may represent a variety of reproductive propagules (Sigler and Carmichael, **1976**; Kendrick and Watling, **1979**).

What is preserved of this fungus is morphologically simple, representing only branched, septate hyphae bearing clamps and chains of spores separated by intercalary hyphal cells. These characteristics suggest only probable affinities with basidiomycetes and possible affinities with ascomycetes, or both. Hypothetically, the formation of meiospores within the spores of *Palaeofibulus* would suggest that it was ascomycetous, while meiospores borne exterior to the spore would imply basidiomycetous relationships. The absence of either spore type precludes definitive classification of this fungus. However, because apparent meiospores are absent in this material we suggest that *Palaeofibulus* may share affinities with the "conidial basidiomycetes," which possess conidium-like spores but lack basidia and basidiospores. Furthermore, it is possible that the thick-walled spores in *Palaeofibulus* may be chlamydospores.

The thick-walled spores of *Palaeofibulus* more closely resemble chlamydospores commonly associated with conidial states rather than teliospores of rusts, which are obligate plant pathogens. Occurrence of *Palaeofibulus* within several plant organs in the peat deposits suggests that this fungus was an opportunistic saprophyte rather than involved in a parasitic relationship with any particular member of the Fremouw Peak flora. It is unlikely that *Palaeofibulus* represents the same clamp-bearing fungus postulated by Stubblefield and Taylor (**1986**) to be one causal agent of Triassic wood rots (white and white pocket rots). Even though these two fungi were collected from the same locality, the rot fungus was apparently a specialized saprophyte, while *Palaeofibulus* appears to have had more generalized nutritional requirements. In addition, the clamp connections produced by both fungi are morphologically dissimilar (cf. Figs. 3, 4; Stubblefield and Taylor, **1986**).

At the present time the nature of the specimens of *Palaeofibulus* preclude its identification with any specific extant forms. Although some similarities could be suggested based upon comparisons with a variety of living morphotypes, we believe such comparisons provide little basis for evaluating the natural affinities of this Triassic fungus. Rather, such identifications become a standard for speculation on the distribution of fungi through geologic time and geographic occurrence, and thus provide dubious information toward discussions of fungal phylogeny and evolution. When limited to the structural characters of fungi, fossil specimens such as *Palaeofibulus* do provide an increasing data base on the diversity of fungi through geologic time. As information about fossil fungi accumulates through discovery of new specimens, the opportunity may be afforded to evaluate evolutionary relationships within major groups and, moreover, the potential for considering general trends in fungal evolution may be realized.

ACKNOWLEDGMENTS

This research was supported in part by the National Science Foundation (BSR-8516323) and represents contribution No. 659 from the Byrd Polar Research Center.

Key Words: *Palaeofibulus antarctica,* fossil fungi, clamp connections, basidiomycetes, Triassic, Antarctica.

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FIGS. 1–8. Vegetative and reproductive features of *Palaeofibulus antarctica.* 1. Fossil mycelium within lacunar canal of a plant axis, ×110. 2. Clamp connection showing septa within clamp (arrow), ×1400. 3. Hyphal strand showing incomplete clamp (I) and well-defined clamp (arrow) along same hypha, ×1400. 4. Section through two spores showing intercalary cell (arrow) and thick spore wall, ×1400. 5. Higher magnification of FIG. 1 showing overall septate, branching hyphae as well as chains of spores, ×425. 6. Septate clamp connection; also note globose spore, ×1400. 7. Ellipsoidal-globose spores, ×1400. 8. Chain of thick-walled spores attached by intercalary cells (arrows), ×880. 1, 2, 4–7. OSU 10216 D top 2$\alpha$; 3. OSU 10216 D top 11$\alpha$; 8. OSU 10216 D top 19$\alpha$.

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*Mycologia*, 81(4), 1989, pp. 626–631.


# A NEW SPECIES OF *TRIADELPHIA* FROM TAIWAN

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*Triadelphia* was erected by Shearer and Crane (**1971**) to accommodate a single species, *T. heterospora*, a saprophyte on balsa wood blocks submerged in the Patuxent River, Maryland. *Triadelphia heterospora* characteristically produces two different forms of conidia; one is cylindrical and 2-septate, the other is broadly obclavate to ellipsoid and 4–7-septate (Shearer and Crane, **1971**). Constantinescu and Samson (**1982**) reexamined herbarium specimens of *T. inquinans* (Sacc.) Hughes & Pirozynski and *T. heterospora* Shearer & Crane and living cultures of *T. loudetiae* Maggi *et al.* and *T. pulvinata* Maggi *et al.* Their studies indicated these species to be highly pleomorphic, possessing 3–5 forms of conidia. Constantinescu and Samson (**1982**) described a new species, *T. romanica*, and transferred *Stemphylium albamensis* Matsushima to *Triadelphia*. They also emended the generic description of *Triadelphia*, redescribed and illustrated all previously documented species and provided a key to six described or newly combined species. Recently, *Dicoccum uniseptatum* (Berk. & Br.) Sacc. was transferred to *Triadelphia* based on conidiogenous cell morphology, conidium ontogeny and conidium morphology, which are all comparable to the six *Triadelphia* species. *Triadelphia uniseptatum* differs from other *Triadelphia* species,